

FLORISTIC DIVERSITY IN THE EXPERIMENTAL
WATERSHEDS OF THE HUBBARD BROOK
EXPERIMENTAL FOREST, NEW HAMPSHIRE, USA

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ABSTRACT. Complete abundance-annotated botanical inventories of managed and unmanaged forested areas provide critical baseline data for the long term monitoring of floristic diversity. Such data are essential in identifying species at risk of local or regional extirpation, in tracking rates of exotic invasion, and in the evaluation of species diversity effects arising from natural and anthropogenic disturbance. The reaction of forest herbaceous species to disturbance, and their subsequent recovery rates, have been little studied to date. This study documents the complete floras of seven experimental watersheds of the Hubbard Brook Experimental Forest, compares their relative floristic characters, and provides baseline data for long term diversity monitoring at the Hubbard Brook Experimental Forest. The two watersheds having undergone experimental clearcuts in the recent past were found to differ significantly in elements of the herbaceous understory. These differences were not reflected in tree data and suggest that forest management policies based on tree recovery times may underestimate true floristic recovery periods, and threaten diversity over the long term.

Key Words: flora, floristic diversity, understory succession, herbaceous recovery, forest ecosystems, Long Term Ecological Reserve, Hubbard Brook Experimental Forest

According to classical theory, secondary succession of the understory in disturbed forests is largely a factor of canopy development and competition (Bormann and Likens 1979; Kimmins 1997). Species richness in secondary forests is believed to be closely tied to successional stages. Theoretically, an increase in diversity is expected in the early stages, followed by a decrease as the canopy closes, followed by another gradual rise as the woodland flora is restored (Bormann and Likens 1979; Kimmins 1997). In New England, Bormann and Likens (1979) observed

that heavily cut hardwood forests initially underwent a dramatic increase in shade-intolerant species, followed by a gradual decline in these species as the canopy developed and light regimes changed. Shade-tolerant species (woodland species) that were able to survive both the loss of the forest canopy and the competitive pressures of the weedy invaders were theorized to be free to increase in abundance once the canopy reached sufficient maturity. Additional woodland species would likely immigrate from surrounding areas and the secondary forest flora would thus, at least in theory, approach and potentially even achieve pre-cut levels of diversity over time.

While the effects of disturbance on floristic diversity have often been speculated upon in the scientific literature, particularly of such catastrophic disturbance as mechanized clearcutting, clear answers continue to elude us (Bratton 1976; Carbonneau 1986; Meier et al. 1995; Peterken and Game 1984; Whitney 1991; Whitney and Foster 1988). Unquestionably, the lack of long term data has inhibited our efforts. The preponderance of data from New England forests have traditionally focused on tree species alone, with understory communities examined only in terms of total biomass or total percent cover in prescribed plots. Studies distinguishing individual herbaceous species are rare, and full inventories of research sites are rarer still.

This study employed complete floristic inventories rather than a plot-based approach because total inventories provide the most accurate measure of species richness, and are therefore best suited for long-term diversity monitoring. While valuable for many applications, plot sampling provides only an estimate of the site's true species richness. Such sampling techniques tend to miss rare species altogether and underestimate contagiously distributed (clumped) species. These restrictions limit the value of plot-based approaches in diversity studies of young forests, where contagious distributions are more common (Kimmins 1997; Whitney 1991), and in mature forests, where rare species have often been found to be among the better indicators of old growth systems (Whitney and Foster 1988). Plots also lack the ability to deal with floristic drift, making local extirpations or introductions difficult to document.

The objectives of this study were to conduct complete inventories of the vascular floras of the Hubbard Brook Experimental Forest (HBEF) watersheds, with population abundance estimates,

and to compare relative floristic similarities between them with respect to past experimental management treatments. These constitute the first complete botanical inventories ever conducted at HBEF and will serve as the baseline for long-term monitoring of floristic diversity, as well as aid in future ecological research within the watersheds.

All the experimental watersheds in the HBEF are secondary forests. This paper focuses on a comparison of the floristic diversity within two watersheds having undergone experimental clearing in the past few decades with that of several of the watersheds consisting of more mature secondary forest.

SITE DESCRIPTION

Study area. The Hubbard Brook Experimental Forest is a 3160 ha Biosphere Reserve in the White Mountain National Forest, New Hampshire, dedicated as a Long Term Ecological Reserve (LTER), and operated by the U.S.D.A. Forest Service's Northeastern Forest Experiment Station. Since the Hubbard Brook Ecosystem Study was founded in 1963, ten small, well-defined experimental watersheds have been delineated in the northeastern section of the bowl-shaped Hubbard Brook Valley. Over 1500 publications have been generated by HBEF researchers, most involving these watersheds, yet complete floristic inventories had never been conducted. Seven of the ten experimental watersheds were inventoried for this study (Figure 1), including five adjacent watersheds on the south- to southeastern-facing slope (W1, W3, W4, W5, W6), located in the town of Woodstock, and two adjacent watersheds on the north-facing slope (W7, W8), located in the town of Ellsworth (Table 1).

The upper portions of most of the watersheds were characterized by a Lyman-Tunbridge soils association or a Tunbridge-Lyman-Rock outcrop complex; the middle third was Beckett series; the lower portion was mostly Berkshire, Marlow, or Peru-Marlow soils (Hubbard Brook Experimental Forest 1996). The watersheds share relatively impermeable bedrock and typical New England acidic, coarse, well-drained soils, derived from glacial tills (Siccamo et al. 1970). Soil texture ranged from fine to very rocky sandy loam and average soil depth was 1.5 m, with shallower soils occupying the upper third of most watersheds. Significant decreases in till depths occurred at 732 m in elevation and above

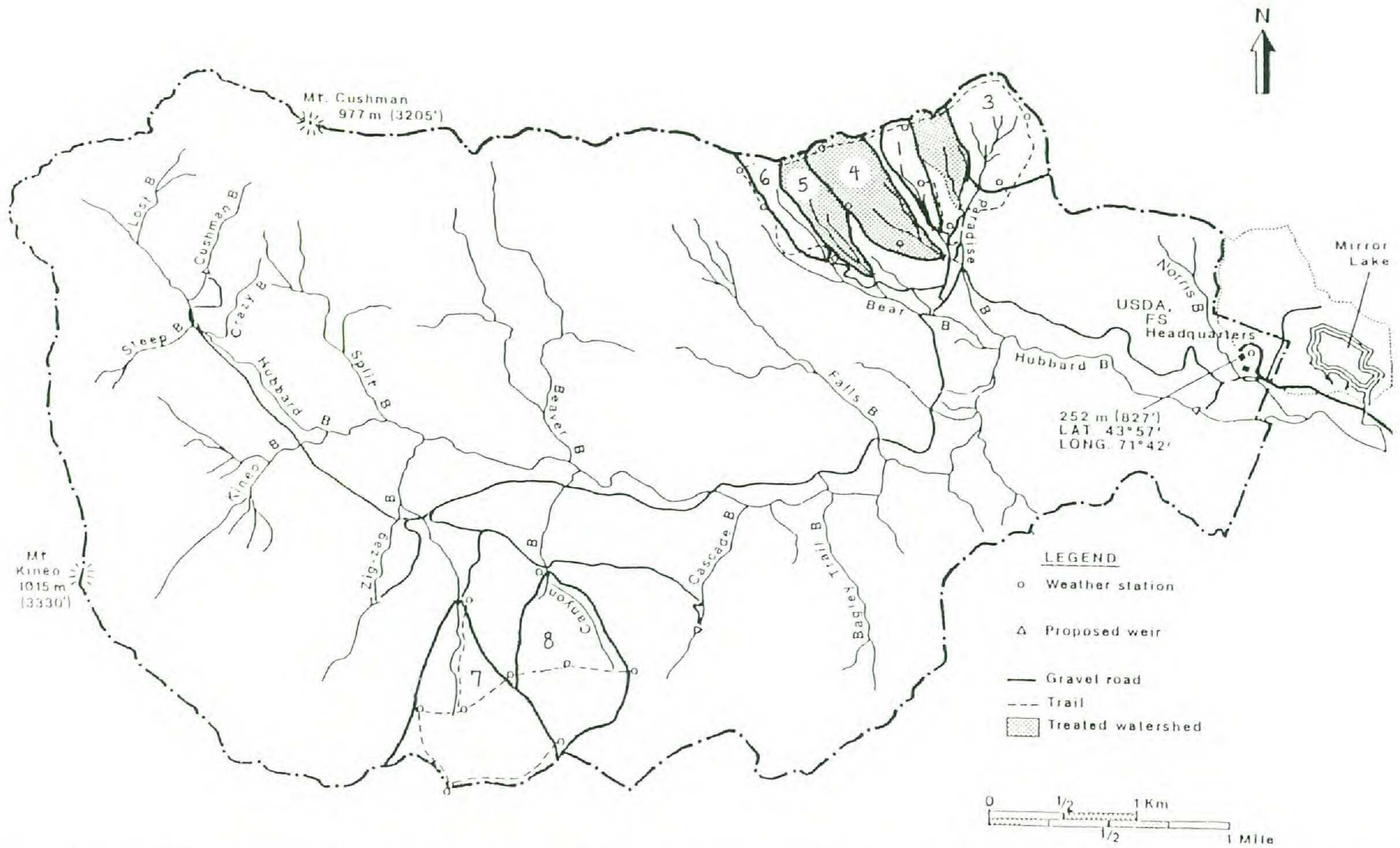


Figure 1. Map of the Hubbard Brook Experimental Forest, showing delineation of the seven experimental watersheds studied. Shading indicates areas that were logged as experimental treatments.

Table 1. Characteristics of the Hubbard Brook experimental watersheds. Percent of total watershed areas attributed as hardwood (HW), mixed hardwood–spruce-fir (CON), and open (OPEN) vegetation class type was determined using the HBEF vegetation map prepared by Cornell University's Resource Information Lab in 1979, and 1987 aerial photography provided by the U.S.D.A. Forest Service, Pemigewasset Station.

| WS | Treatment | Slope Aspect | Elevation (m) | Area (ha) | HW % | CON % | OPEN % | Total Species Richness |
|----|-----------------------|--------------|---------------|-----------|------|-------|--------|------------------------|
| 1 | Noncutting treatments | S23W | 527–732 | 11.8 | 78.0 | 16.4 | 5.6 | 73 |
| 3 | Reference | S22E | 488–747 | 42.2 | 84.3 | 13.6 | 2.1 | 75 |
| 4 | Strip cut 1970–74 | S40E | 442–747 | 36.1 | 93.8 | 3.0 | 3.2 | 89 |
| 5 | Clearcut 1983–84 | S24E | 488–762 | 21.9 | 87.2 | 1.0 | 11.8 | 114 |
| 6 | Reference | S32E | 549–792 | 13.2 | 75.3 | 22.9 | 1.8 | 61 |
| 7 | Reference | N16W | 619–899 | 76.4 | 58.6 | 40.4 | 1.0 | 94 |
| 8 | Reference | N12W | 610–905 | 59.4 | 34.2 | 64.8 | 1.0 | 71 |

(Bormann et al. 1970; Federer et al. 1990). At high elevations exposed bedrock was common, but rock outcrops and occasional large boulders occurred at all elevations throughout the Hubbard Brook Valley. The valley was characterized by rather oligotrophic nutrient conditions.

The Hubbard Brook Valley is described by mesic, cool-temperate, humid continental conditions (Whittaker et al. 1974). For more detailed information on the climate of HBEF see Hubbard Brook Ecosystem study site description and research activities (Hubbard Brook Experimental Forest 1996).

Prior to 1895, most of the Hubbard Brook Valley was mature, primary forest (Bormann et al. 1970; Likens and Bormann 1995). The valley was intensively logged between 1895 and 1917 with no evidence of further logging activity or fire after this time. The valley did not experience any serious damage as a result of the 1938 hurricane (C. Cogbill, HBEF researcher, pers. comm.). At the time of this study, the watersheds were characterized by relatively even-aged secondary forests with some older trees present. Two of the watersheds inventoried (W4, W5) were experimentally clearcut within the last thirty years and, hence, were young, even-aged tertiary forests.

Three intergrading vegetation types existed in the experimental watersheds: northern hardwood forest, mixed hardwood–spruce-fir forest, and open areas. Northern hardwood forest typically occupied the lower elevations (440–670 m), and was characterized by the dominant tree species *Fagus grandifolia*, *Acer saccharum*, and *Betula alleghaniensis*, with less abundant populations of *Fraxinus americana*, *A. pensylvanicum*, *A. rubrum*, and *A. spicatum*. Understory vegetation tended to be abundant in these areas and typical shrub species included *Lonicera canadensis*, *Cornus alternifolia*, and *Viburnum alnifolium*. Herbaceous species such as *Dryopteris intermedia*, *Smilacina racemosa*, *Trillium erectum*, *T. undulatum*, *Streptopus roseus*, and *Uvularia sessilifolia* were commonplace on the forest floor. Slopes ranged from 10° to 30°.

Boreal spruce-fir vegetation began to intergrade with the hardwood forest at around 670 m, as well as occurring on mid-to-high elevation rocky outcrops. Trees characterizing the boreal spruce-fir vegetation type include *Abies balsamea*, *Picea rubens*, and *Betula cordifolia*, with less abundant populations of *B. alleghaniensis* and *Sorbus americana*. Understory vegetation was typically less abundant than in pure hardwood areas and could include large areas with virtually no ground flora at all. Shrub species typical of this intergraded forest type included *Viburnum alnifolium*, *Vaccinium myrtilloides*, and *V. angustifolium*. Characteristic herbaceous species included *Dryopteris campyloptera*, *Coptis trifolia*, *Cornus canadensis*, and *Lycopodium obscurum*. These forests were characterized by shallower soils than pure hardwood regions, a decrease in mean temperatures, increased wind stress and precipitation, a reduced growing season (longer periods of snow cover and shorter frost-free periods), and generally more rugged terrain. Slopes of up to 30° were common.

Open areas in the watersheds were primarily represented by the 0.3 ha rain gauge clearings and particularly wide portions of the foot trails, both maintained in the watersheds for the purpose of hydrological research. In a very few cases the floras of small, naturally occurring open areas fell within this vegetation category, although such areas were not common in the HBEF watersheds. An open area was defined as any breach in the canopy of over 10 m², regardless of elevation, estimated by field observer's strides. Tree species in these areas were thus limited primarily to stump shoots (in rain gauge clearings and areas of recently clear-

cut forest) and seedlings of taxa defining either of the two previous vegetation types. Herbaceous species varied widely from site to site, a fact which likely reflected the combined influences of seed bank, surviving woodland species occurrences, and species introductions by human traffic.

Watershed descriptions. Five watersheds were considered “references” for the floristic comparisons in this study; two underwent experimental harvesting treatments in the recent past. Reference watersheds W1, W3, W6, W7, and W8 were last cut in the early 1900s and were hence maturing secondary forests at the time of this study (Table 1). Watershed 1, while designated here as a reference, underwent experimental applications of calcium in the year after its inventory was complete. Watershed 3 encompassed the largest proportion of pure hardwood forest among these references and additionally benefitted from a diverse network of streams and tributaries.

The watershed most frequently used as a vegetation reference by other HBEF researchers (Wayne Martin, HBEF Site Supervisor, pers. comm.) was W6. Its stand composition had been referred to as reasonably representative of climax conditions (Bormann et al. 1970), and its ecological systems had been assessed as mature and in dynamic balance, based upon vegetation biomass and productivity data (Leak 1987; Siccama et al. 1970; Whittaker et al. 1974). An HBEF policy of minimal disturbance of W6 has resulted in the absence of rain gauge clearings, limited foot traffic, and the prohibition of plant collecting within this watershed.

Reference W7 was the largest watershed in the study and had a great variety of observed microhabitats (defined here as specialized areas within the larger habitat, occupied by uniquely different taxa or taxonomic groups). Some examples included several small wetlands not found elsewhere in the study, and numerous small cascades which created stifles and vernal pools throughout both hardwood and mixed coniferous areas. Reference W8 stood somewhat apart from the other watersheds floristically, due to its significantly smaller percent of pure hardwood area (Table 1).

Treatment watersheds W4 and W5 were both young tertiary forests recovering from clearcutting treatments. Watershed 4 was experimentally cut during the winters of 1970 through 1974. A “progressive strip cut” method was used and resulted in the wa-

tershed's total clearance. The watershed was divided into 49 roughly parallel strips, each 25 m wide and oriented east to west along the contours of the slope. In the fall of 1970 every third strip was cut, constituting the first of the series. All merchantable trees were removed from the site and scarification of the soil was encouraged by varying skidder routes across the active strips. In the fall of 1972, the series of strips below the first were cut, and the remaining trees were harvested in the fall of 1974. A more detailed account of this watershed treatment is presented by Martin and Hornbeck (1989).

At the time of this study, W4 was a 26-year-old tertiary forest dominated by dense, relatively even-aged stands of *Prunus pensylvanica*, *Acer pensylvanicum*, *Fagus grandifolia*, and *Betula alleghaniensis*. The canopy was dense and continuous relative to the other watersheds, and consequently, light levels in this watershed may have been lower. While forest undergrowth tended to be sparse, invasive shade-intolerant species persisted from when this watershed was first cleared, and were in evidence wherever the canopy was broken.

Watershed 5 was mechanically whole-tree clearcut over the winter of 1983–84. Once again, all merchantable trees were removed and mechanical scarification of the soil was encouraged. Only limbs and treetops were left on site, resulting in the removal of more than 90% of the aboveground biomass.

At the time of this study, W5 was a 16-year-old tertiary forest dominated by even-aged *Prunus pensylvanica*, *Acer pensylvanicum*, *Fagus grandifolia*, and *Betula alleghaniensis*. Tree regeneration was heavy, making foot travel through this site difficult. The canopy was well developed, however the remains of primary skidder trails were still evident, constituting some of W5's substantial area of open canopy, relative to both reference watersheds and W4. Watershed 5 was also observed to offer a good variety of microhabitats due in part to its topographic heterogeneity. One example of this was a small, well-developed wetland, which was likely iced over during the harvesting operations, and therefore survived relatively intact.

MATERIALS AND METHODS

Reconnaissance field surveys were used to inventory the flora of each watershed according to three vegetation classes: hard-

Table 2. Frequency of occurrence scale suggested by Palmer et al. 1995. A “dominant” species was defined as one constituting approximately 20% or more of all individuals present. “Individuals” of clonal species were defined as ramets.

| Rank | Category | Qualitative Description |
|------|------------|---|
| 5 | Abundant | Dominant or codominant in one or more common habitats |
| 4 | Frequent | Easily seen or found in one or more common habitats, but not dominant |
| 3 | Occasional | Widely scattered, but not difficult to find |
| 2 | Infrequent | Difficult to find, few individuals or colonies, but found in several locations |
| 1 | Rare | Very difficult to find and limited to one or very few locations or uncommon habitats |
| 0 | Absent | Not found, but found in a previous survey from the same or similar sites, or was otherwise suspected to occur |

wood forest, mixed hardwood–spruce-fir forest, and open areas. Separate inventories were taken for each of these three classes within each of the seven watersheds. The mixed hardwood–spruce-fir forest category represented both areas of pure spruce-fir type vegetation, and the boundary where the spruce-fir and northern hardwood forest types intergraded. This class was identified by a combined presence of 40% or more of *Picea rubens* and *Abies balsamea* in the canopy.

The first weeks of spring (early May) were spent mapping microhabitats and dividing the vegetation classes into segments that could be readily traversed in a field day. These segments were then visited weekly from mid-May through early September. Watersheds 1, 3, 4, 5, and 6 were surveyed during the field seasons of 1995 and 1996; W7 and W8 were surveyed in 1997. Species lists were compiled and voucher specimens were collected, unless doing so would have threatened the existing population. Collections were deposited in the Hodgdon Herbarium (NHA) at the University of New Hampshire, and in numerous cases, duplicates were placed in the Hubbard Brook collection as well.

Estimates of species abundance within each segment were made based upon the rank abundance approach suggested by Palmer et al. (1995; Table 2). This system was used to rank the frequency of occurrence of individuals of a species in relation to the total flora. A “dominant” species was defined as one consti-

tuting roughly 20% or more of the individuals present. In a highly diverse area it was therefore possible to have no species rate in the “abundant” category (5), but rather, several rated only as “frequent” (4). Due to the prevalence of clonal species in this study, “individuals” were defined as ramets. At the end of the field season, data from all segments constituting a watershed’s vegetation class were combined. The proportional area the segment represented was calculated and estimates of species abundance were averaged according to that proportion, yielding an estimate for the entire vegetation class.

Data were analyzed both by vegetation class and total watershed. Total floras were examined compositionally by tree, shrub, and herbaceous communities, and the herbaceous community was further divided into “woodland” and “nonwoodland” species (Teeling 1998). The definition of “woodland species” is adapted from a Peterken and Game (1984) analysis, which partitioned “shade-casters, shade-bearers, and wood-margin species” (p. 159) into a group seen as more representative of undisturbed forests. In this study, we have included forest gap species in the woodland species list. “Nonwoodland” species were thus the shade-intolerant species more associated with open areas or early successional conditions.

Sørensen’s Index of Similarity, expressed as a percentage, was used to compare the watersheds’ total floras. This index measures the number of coinciding species occurrences against the number of theoretically possible co-occurrences (Mueller-Dombois and Ellenberg 1974). The index is described by:

$$IS_s = \frac{2c}{a + b} \times 100$$

where a is the number of species in area A, b is the number of species in area B, and c is the number of species in common to both areas A and B.

The seven watersheds, each with three vegetation classes, produced 21 “study units” with species richness and corresponding abundance data (Table 3). Analysis of covariance (ANCOVA) was used to examine relationships between watershed and vegetation class (both classification data), and species richness in these units, while adjusting for any effects of area (continuous data; Ostle and Mensig 1975). Total species richness was the dependent

Table 3. Area and total species richness of the 21 “study units”, representing the hardwood (HW), mixed hardwood–spruce-fir (CON), and open (OPEN) vegetation classes within each of the seven watersheds.

| | Study Unit | Area (ha) | Total Species Richness |
|----|------------|--------------|---------------------------|
| 1 | HW1 | 9.2 | 55 |
| 2 | HW3 | 35.7 | 63 |
| 3 | HW4 | 33.8 | 69 |
| 4 | HW5 | 19.1 | 90 |
| 5 | HW6 | 9.9 | 53 |
| 6 | HW7 | 44.7 | 74 |
| 7 | HW8 | 20.3 | 60 |
| 8 | CON1 | 1.9 | 54 |
| 9 | CON3 | 5.8 | 47 |
| 10 | CON4 | 1.1 | 41 |
| 11 | CON5 | 0.2 | 60 |
| 12 | CON6 | 3.0 | 30 |
| 13 | CON7 | 30.9 | 65 |
| 14 | CON8 | 38.5 | 44 |
| 15 | OPEN1 | 0.66 | 47 |
| 16 | OPEN3 | 0.87 | 53 |
| 17 | OPEN4 | 1.16 | 54 |
| 18 | OPEN5 | 2.60 | 74 |
| 19 | OPEN6 | 0.25 | 23 |
| 20 | OPEN7 | 0.80 | 65 |
| 21 | OPEN8 | 0.60 | 52 |

variable, area was the independent covariate, and watershed and vegetation class were the independent noncomitant variables. Four subsets of species richness were also tested to examine possible associations to watershed characteristics. These were tree species, herbaceous species, woodland herbaceous species, and nonwoodland herbaceous species. There was insufficient replication to include interaction terms in these analyses. Protected Tukey’s pairwise comparison tests were used to identify differences between individual watersheds.

As species richness is only a presence-absence indicator, population sizes of tree, herbaceous, woodland, and nonwoodland species within the watersheds were compared via abundance rank distribution patterns. These comparisons were made by hardwood and mixed hardwood–spruce-fir vegetation class and were viewed as a way of comparing the general establishment and vigor of individual species populations in the tree, total herbaceous, and

woodland herbaceous subsets. Open areas were not analyzed. Species were sorted according to abundance ranks into four categories (due to the scarcity of data in abundance ranks 4 and 5, these two ranks were combined). Chi-square test for independence was used to compare abundance distribution patterns of species in each of the watersheds.

RESULTS

One hundred and fifty-five species were encountered in the combined 261 ha of the seven experimental watersheds, only 3.2% of which (or five species) were non-native (Appendix). Eighty-three of those species, or 70.3% of all herbaceous species, were designated as woodland herbaceous species. Clearcut watershed W5 was richest overall, while W6 was least rich (Table 1). In all watersheds and in each of the three vegetation classes, the herbaceous community proved to be far richer than either the tree or shrub communities, with hardwood areas showing the greatest herbaceous diversity overall (Figures 2 and 3).

Analysis of Variance (ANOVA) testing, using watershed area as the independent variable and species richness as the dependent variable, indicated that area was not a significant factor in determining species richness within the watersheds. Sørensen's Index of Similarity showed strong floristic affinities between the reference watersheds, and lesser affinities between the references and treatment watersheds. Treatment watersheds W4 and W5 were about as similar to one another (74.3%) as the references were to each other (mean 76.0%). The total range of floristic similarity (Table 4) was between 85.3% (W1 and W3) and 59.8% (W5 and W6).

While no significant variables were identified in the ANCOVA using tree species alone, all analyses that included herbaceous species data provided significant results (Table 5). In successive ANCOVAs using the total species list, herbaceous species only, and woodland herbaceous species only, both watershed and vegetation class proved to be significantly associated with species richness. Watershed was the only variable significantly associated with nonwoodland herbaceous species richness. Area was not a significant predictor of species richness in any of the datasets used. Results of protected Tukey's pairwise comparison tests most often revealed significant differences in species richness between

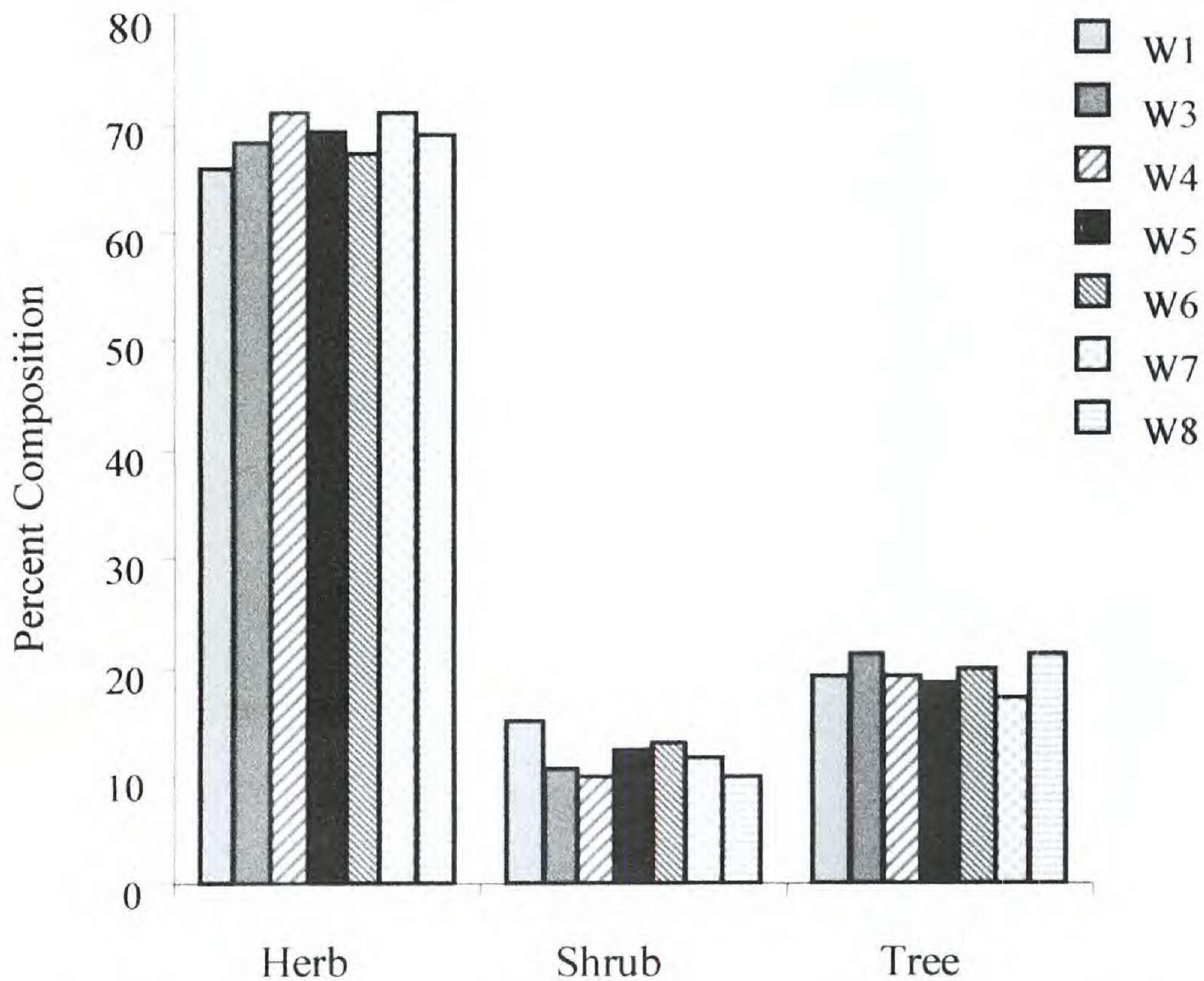


Figure 2. Percent composition of total watershed floras dominated by the herbaceous, shrub, and tree communities.

treatment watersheds W4 and W5, and the two references representing richness extremes: W6 being the least rich, and W7 being the richest (Table 6).

Comparisons of rank abundance distribution patterns of tree species revealed no statistically significant differences in forested regions of the seven watersheds, according to Chi-square tests for independence (Table 7). In contrast, distribution patterns of both herbaceous and woodland herbaceous species in hardwood regions were found to differ significantly across the watersheds (Figures 4 and 5). Removal of W5 data from the herbaceous analysis resulted in the loss of significance, while removal of W4, W5, or W7 all resulted in reversing test results in the woodland herbaceous species analysis.

DISCUSSION

As watershed area was not found to be a significant factor affecting species richness, floristic differences between the seven

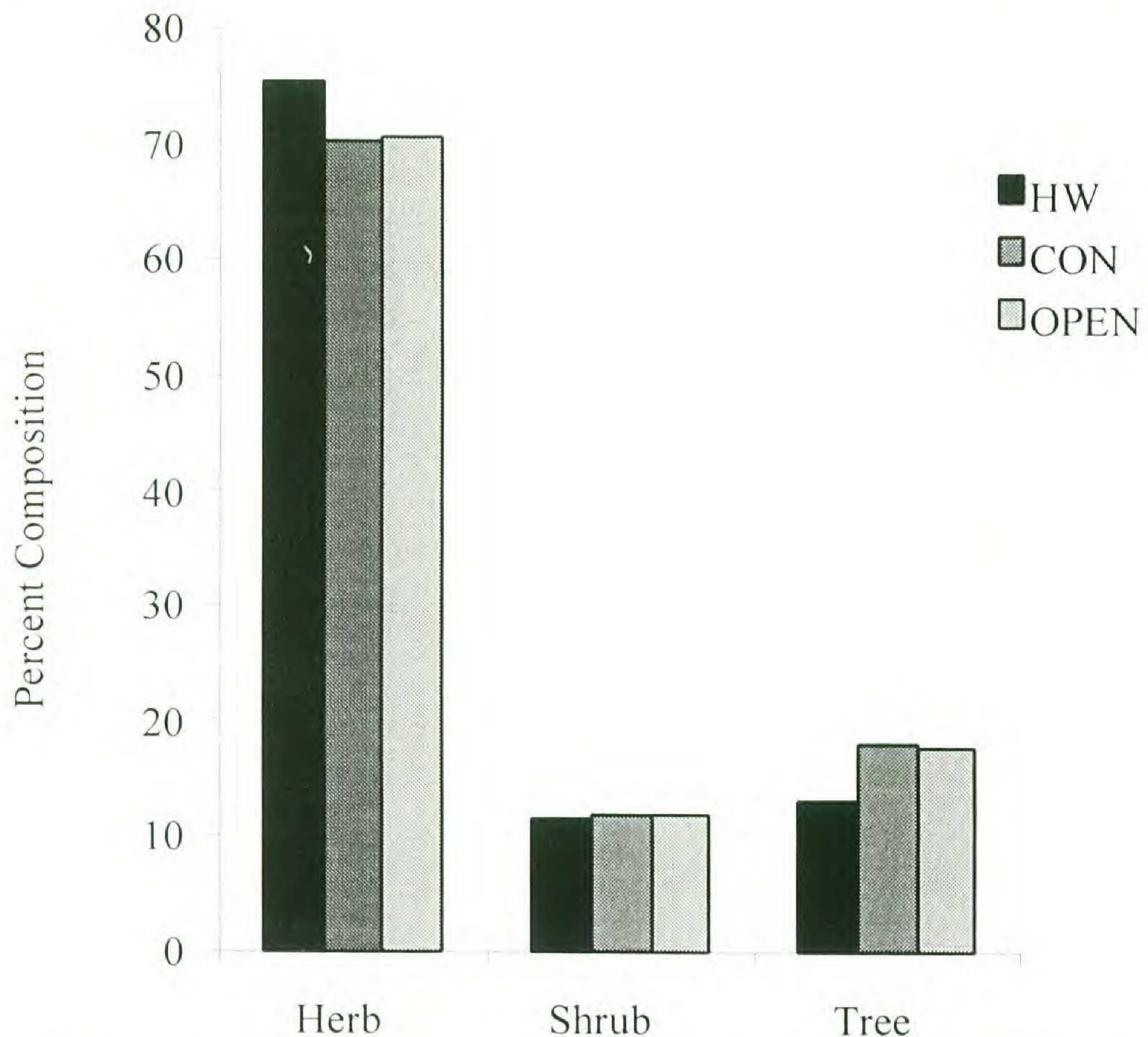


Figure 3. Percent composition of the hardwood (HW), mixed hardwood–spruce–fir (CON), and open (OPEN) vegetation class floras dominated by the herbaceous, shrub, and tree communities.

Table 4. Sørensen's Index of Similarity matrix for the watersheds studied. Main diagonal (bold) is the number of species in each watershed, above the main diagonal is the number of species in common to both watersheds, and below the main diagonal is Sørensen's percent floristic similarity. Mean similarity is 73.5%. Standard deviation from the mean is 5.57%.

| | W1 | W3 | W4 | W5 | W6 | W7 | W8 |
|----|-----------|-----------|-----------|------------|-----------|-----------|-----------|
| W1 | 68 | 61 | 62 | 62 | 49 | 58 | 52 |
| W3 | 85.3 | 75 | 65 | 65 | 52 | 62 | 54 |
| W4 | 79.5 | 79.8 | 88 | 75 | 54 | 63 | 59 |
| W5 | 68.1 | 68.8 | 74.3 | 114 | 52 | 73 | 60 |
| W6 | 76.6 | 77.0 | 73.0 | 59.8 | 61 | 54 | 49 |
| W7 | 72.5 | 74.3 | 70.0 | 70.9 | 71.1 | 92 | 65 |
| W8 | 74.8 | 74.0 | 74.2 | 64.9 | 74.8 | 79.8 | 71 |

Table 5. Results of linear ANCOVA models for tree, total, herbaceous, woodland herbaceous, and nonwoodland herbaceous species richness (S), and noncomitant variables area (A), watershed (W), and vegetation class (VC).

| | $S = A+W+VC+k$ | $S = W+VC+k$ | $S = W+k$ | $S = VC+k$ |
|-------------|---|--|------------------------------------|-------------------------------------|
| Tree | $R^2 = 0.411$ A ($p = 0.477$) W ($p = 0.496$) VC ($p = 0.918$) | | | |
| Total | $R^2 = 0.899$ A ($p = 0.953$) W ($p < 0.001$) VC ($p = 0.005$) | $R^2 = 0.899$ W ($p < 0.001$) VC ($p < 0.001$) | $R^2 = 0.639$ W ($p = 0.013$) | $R^2 = 0.260$ VC ($p = 0.066$) |
| Herbaceous | $R^2 = 0.898$ A ($p = 0.898$) W ($p = 0.001$) VC ($p = 0.003$) | $R^2 = 0.898$ W ($p < 0.001$) VC ($p < 0.001$) | $R^2 = 0.581$ W ($p = 0.033$) | $R^2 = 0.317$ VC ($p = 0.032$) |
| Woodland | $R^2 = 0.907$ A ($p = 0.793$) W ($p = 0.003$) VC ($p = 0.001$) | $R^2 = 0.906$ W ($p < 0.001$) VC ($p < 0.001$) | $R^2 = 0.478$ W ($p = 0.114$) | $R^2 = 0.428$ VC ($p = 0.007$) |
| Nonwoodland | $R^2 = 0.873$ A ($p = 0.555$) W ($p < 0.001$) VC ($p = 0.038$) | $R^2 = 0.868$ W ($p < 0.001$) VC ($p = 0.033$) | $R^2 = 0.768$ W ($p = 0.001$) | $R^2 = 0.100$ VC ($p = 0.386$) |

Table 6. Tukey's pairwise comparison test results for total, herbaceous, woodland herbaceous, and nonwoodland species richness.

| | Significant Watershed Comparisons | <i>p</i> Value |
|-------------|-----------------------------------|----------------|
| Total | W5 and W6 | $p < 0.001$ |
| | W6 and W7 | $p < 0.001$ |
| Herbaceous | W5 and W6 | $p < 0.001$ |
| | W6 and W7 | $p < 0.001$ |
| Woodland | W4 and W7 | $p < 0.001$ |
| | W6 and W7 | $p < 0.001$ |
| Nonwoodland | W1 and W5 | $p < 0.001$ |
| | W3 and W5 | $p < 0.001$ |
| | W5 and W6 | $p = 0.001$ |
| | W5 and W7 | $p = 0.001$ |
| | W5 and W8 | $p = 0.001$ |

watersheds were assumed to be dependent on treatment, stand age, aspect, and environmental site conditions. Overall, the seven watersheds showed a generally high degree of floristic similarity. This was expected for largely contiguous parcels within the HBEF. That the similarity between treatment watersheds W4 and W5 was slightly lower than the mean similarity between the five references (which included noncontiguous areas, with both north- and south-facing aspects) probably reflects W4 and W5's different

Table 7. Chi-square test for independence results for abundance rank distributions of tree, total herbaceous, woodland herbaceous, and nonwoodland herbaceous species in the HBEF watersheds. Floras were analyzed by hardwood (HW) and mixed hardwood–spruce-fir (CON) vegetation classes. Critical value was 37.16.

| | Vegetation Class | χ^2 | Significance |
|-------------|------------------|----------|--------------|
| Tree | HW | 23.33 | No |
| | CON | 10.48 | No |
| Herbaceous | HW | 42.49 | Yes |
| | CON | 23.90 | No |
| Woodland | HW | 40.04 | Yes |
| | CON | 28.73 | No |
| Nonwoodland | HW | 5.11 | No |
| | CON | 4.08 | No |

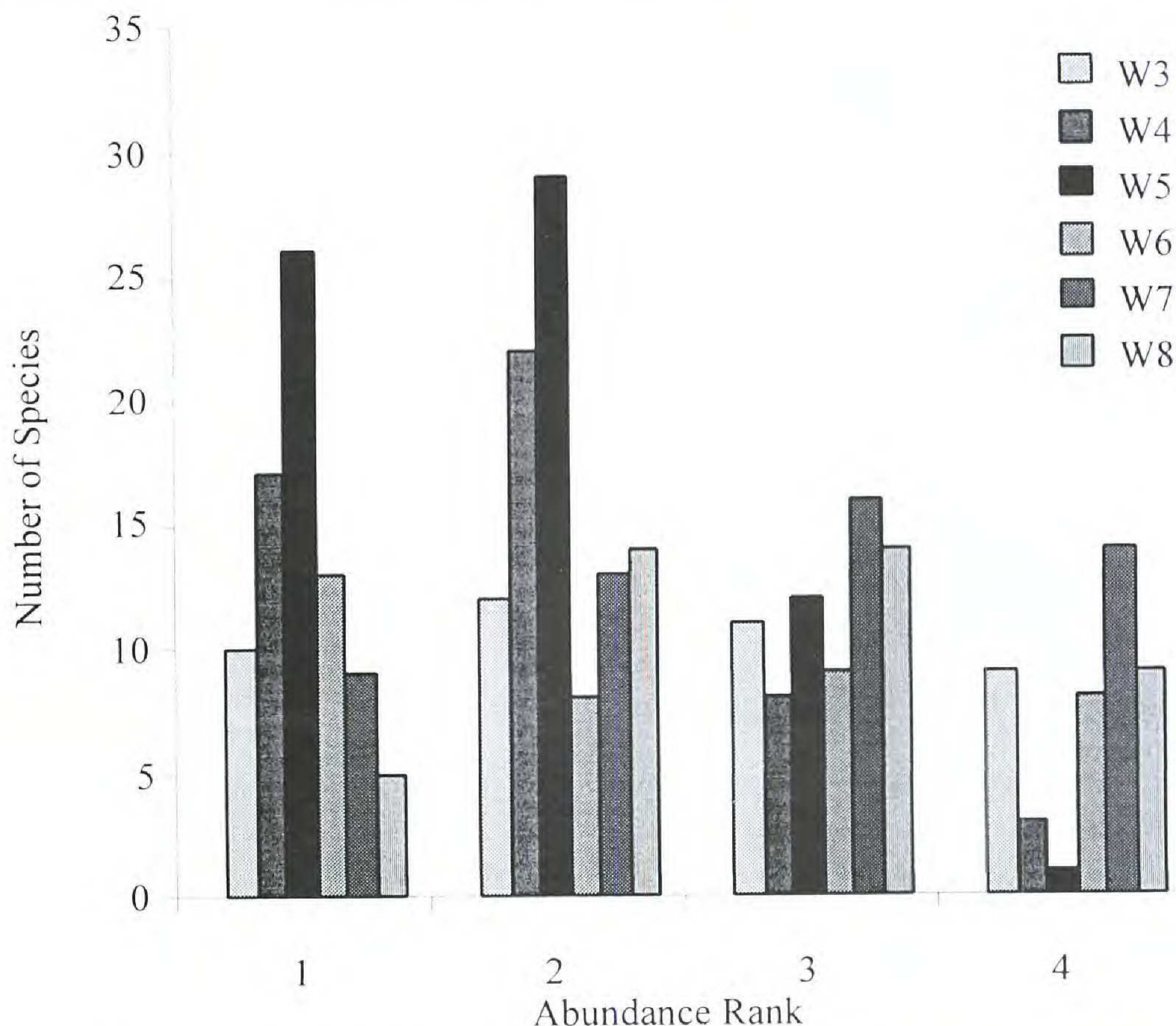


Figure 4. Abundance rank distributions of the herbaceous community in hardwood portions of the watersheds.

successional ages, immigration pool opportunities, and habitat heterogeneity.

Watershed 4 is ten years older than W5 in successional age. Its dense canopy of *Prunus pensylvanica* had largely occluded light from the forest floor, a state witnessed by both the lower occurrence and abundance of shade-intolerant herbaceous species in its flora. According to theoretical expectations, W4 may have experienced a drop in species richness as the result of a transition taking place between the shade-intolerant species, which had dominated since the site was first cleared, and the woodland herbaceous species, which will persist through further canopy development (Bormann and Likens 1979). In contrast, W5's flora was still marked by a higher number of sun-loving, nonwoodland herbaceous species surviving in its less-mature canopy conditions.

It is also possible that W5's richer initial "source pool" for nonwoodland species (namely the adjacent W4, which had been

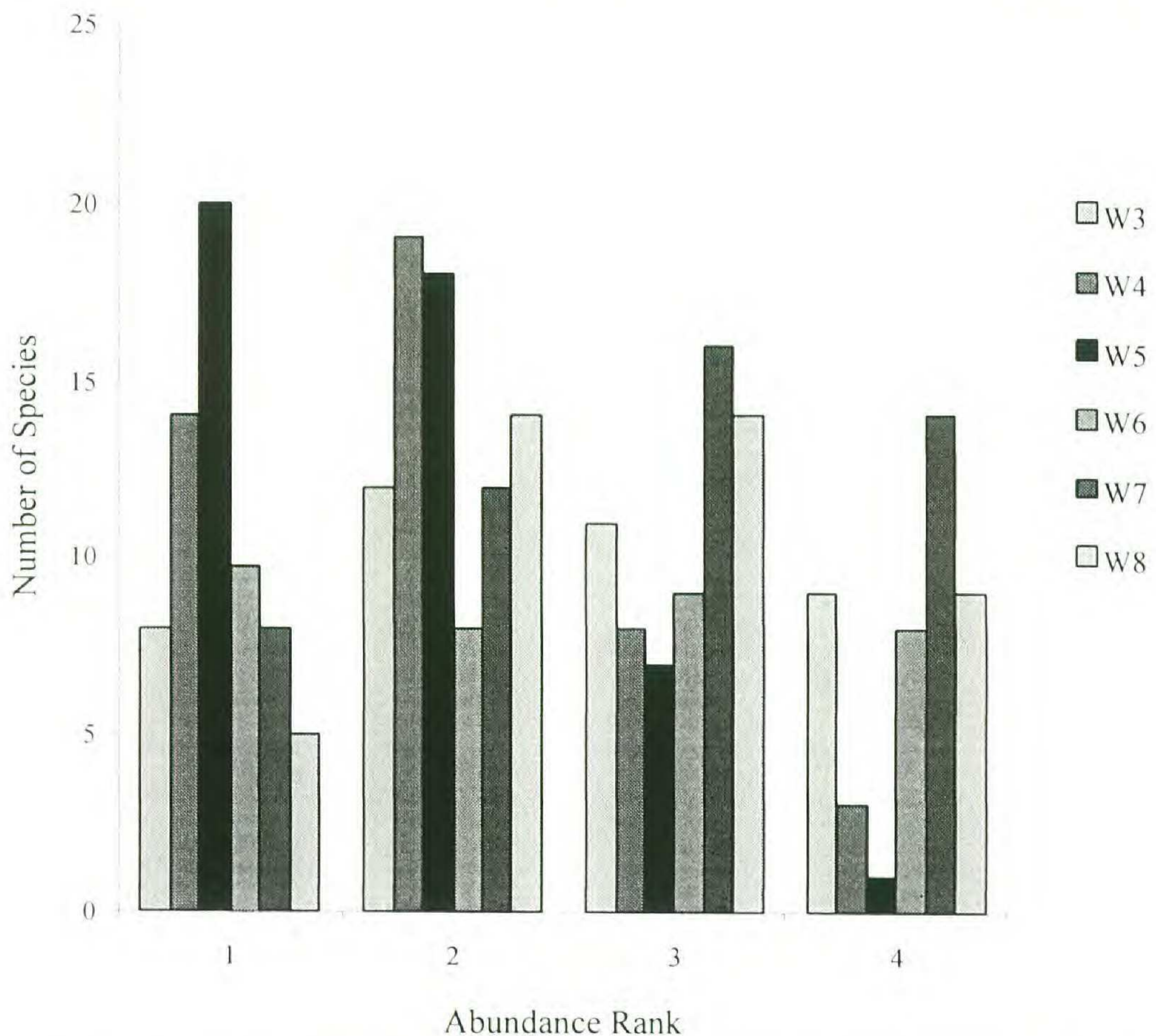


Figure 5. Abundance rank distributions of the woodland herbaceous flora in hardwood portions of the watersheds.

cleared ten years earlier) allowed W5 to develop a richer flora of shade-intolerants in the earliest stages of its succession than W4 (MacArthur and Wilson 1963). All but two of the nonwoodland species found in W4 were also found in W5 (*Festuca ovina* and *Lactuca hirsuta*). Situated as it was between the heavily forested W6 and W5 at the time of its clearing, it seems unlikely that W4 would have had access to the same source pool of shade-intolerant propagules, and so, its early flora may have been poorer than W5's even initially.

Lastly, the differences between the floras of W4 and W5 may be more an inherent factor of the watersheds themselves than any factor of treatment. W5's relatively high habitat diversity may well have resulted in a richer flora than that of W4, even before their treatments. It should be noted that since floristic inventories of W4 and W5 were not conducted before their experimental

clearings, it is impossible to know the level of similarity between their original floras.

Floristic comparisons between the watersheds were further examined by vegetation class, where area was once again found to be insignificant by ANCOVA testing (Table 5). Our initial investigation explored the viability of using tree species data alone to represent HBEF vegetation. While the seven watersheds followed the same rank order in tree species richness as was seen in total species richness, no statistically significant results were produced in the analyses using tree species data alone. No significant relationships were detected between tree species richness and watershed, nor between tree species richness and vegetation class. Combined, these two variables encompassed such inherent site factors as soils, moisture gradients, aspect, treatment history, and habitat diversity. In contrast, these factors were found to be significantly related to total species richness, herbaceous species richness, woodland herbaceous species richness, and nonwoodland herbaceous species richness. This disparity both reflects the reality that New England hardwood and mixed hardwood–spruce–fir forests are composed predominantly of herbaceous species (Bormann and Likens 1979; Kimmins 1997; Westveld et al. 1956), and suggests the possibility that herbaceous species possess an increased sensitivity to aspects of their physical environment relative to woody taxa (Bratton 1976; Carbonneau 1986; Meier et al. 1995; Whitney 1991; Whitney and Foster 1988).

The concept that tree species and herbaceous species recovery from disturbance might be dissimilar is supported by a small body of published research (Crozier and Boerner 1984; Meier et al. 1995; Peterken and Game 1984), but the subject is very much in need of further scientific attention. The forest's herbaceous species differ in a number of ways from trees and shrubs. The most basic differences of scale, which can affect life span, growth and reproduction rates, seed dispersal ranges, rooting breadths, and population-to-area ratios (which lend the increased risk of local extinction), as well as greater reliance on forest floor qualities and microclimate (Bratton 1976; Carbonneau 1986; Meier et al. 1995; Whitney 1991; Whitney and Foster 1988), suggest that herbaceous species may be more impacted by certain forms of disturbance than are woody species. Reliance on tree data alone should therefore be avoided when inferring larger patterns of forest disturbance or recovery.

Tukey's comparison testing (Table 6) revealed that W6, the watershed generally regarded as best representing mature HBEF vegetation, actually represented the low end diversity extreme of the seven watersheds tested. However, W6's flora had a number of unique woodland species (among them *Botrychium oneidense*, *Panax trifolius*, and *Platanthera orbiculata*) as well as markedly abundant populations of most species. Such evidence supports previous studies, which have suggested that this watershed may represent one of the most stable ecosystems examined in this study, nearing or at floristic equilibrium (Bormann et al. 1970; Leak 1987; Whittaker et al. 1974).

Comparison testing also helped identify a critical difference between the highly diverse floras of W5 and W7. While both these watersheds contained significantly richer total and herbaceous floras than W6 (the low-end diversity extreme), W5's flora was not found to be significantly different than W6's in woodland herbaceous species comparisons. This result indicates that, while the flora of W5 was relatively diverse in herbaceous species overall, this diversity is not reflected in the woodland component. As further verification, the flora of W5 was found to be significantly richer than all the other watersheds in nonwoodland species. Thus, W5's diversity can be attributed to the influx of shade-intolerant species that invaded when the watershed was cleared, many of which will not survive further canopy development, while W7's flora is diverse in forest-adapted species.

The apparent similarity between W4's and W6's significantly depauperate woodland floras is also misleading (Table 6). Both watersheds were identified as significantly less rich than W7 (the high end diversity extreme), thereby marking them both as low end diversity extremes. But, it should be recalled that the flora of W6 is significantly depauperate overall, while that of W4 is the third richest watershed in the study. Reviewed in that perspective, W4's overall diversity must also be attributable to the shade-intolerant herbaceous species persisting in its flora. Its significant lack of woodland species seems likely to be a factor of successional age and/or treatment history but, as previously stated, conclusions are difficult to draw as no inventory of W4 was available from before its treatment.

The investigation of species abundance rank distributions again revealed the importance of herbaceous species in assessing overall floristic trends. While tree species abundance did not signifi-

cantly differ across the watersheds, abundance of herbaceous and woodland herbaceous populations was heterogeneous across the hardwood regions of the watersheds (as these are nested data sets, most of the significance in the herbaceous analysis is probably attributable to differences in the woodland herbaceous flora). Since removal of W4, W5, or W7 from the woodland analysis resulted in a loss of significance, it can be inferred that it is these three watersheds that differed significantly from one another in some combination, or combinations. As Figure 5 revealed, W4 and W5 shifted towards the low abundance end of the ranked scale, while W7 is shifted towards the high end. Thus, these significant differences must lie between W7 and the treatment watersheds. Clearly then, W4's and W5's skewed distributions indicate a trend toward smaller population sizes of woodland herbaceous species than those found in reference areas, and significantly smaller populations than those found in W7 (the high-end extreme).

Watersheds with a high percentage of their species in low abundance may possess a high degree of habitat heterogeneity, where the pattern may be reflecting the presence of numerous small microhabitats. Both W5 and W7 encompassed a number of distinct niches not found in the other watersheds of this study. For instance, only these two watersheds possessed well-developed wetland communities (with distinctly different floras). Alternatively, such a pattern may be indicative of a flora with active directional changes taking place. MacArthur and Wilson (1963) defined biological equilibrium as the point at which species immigrations equaled species extinctions. Low population size may indicate a species newly immigrated, or soon to be extirpated from an area. Hence, a flora with a large number of these types of populations may be at floristic disequilibrium, or undergoing an active floristic transition of some kind. Certainly, the early successional floras of W4 and W5 can be characterized in this way.

While species richness was clearly higher for the two clearcut watersheds in the early stages of recovery, the additional species in both cases appeared to be shade-intolerant herbaceous species, most of which will be unlikely to survive further canopy development. In contrast, the population sizes of woodland herbaceous species in these disturbed watersheds were notably lower than reference populations, a condition particularly noteworthy in the

case of W4, whose woodland flora was found to be significantly depauperate as well. Without inventories of these watersheds from before their treatments, it is impossible to know whether these floristic differences are the result of mechanized logging treatments, successional age differences, and/or intrinsic site differences.

There is a great need for floristic studies of New England forests that employ total inventories. Without studies that include detailed herbaceous community data, the possible decline or extirpation of "sensitive" species, rates of exotic species invasion, and effects of timbering, fragmentation, pollution, and other human disturbance on species diversity cannot be accurately assessed. The initial impact of disturbance, as well as the time required to recover stable population sizes, is likely different for the herbaceous and tree communities. Current timber rotation times are based only on tree species recovery, yet it is typically the herbaceous community that most strongly influences diversity overall. Such differences must be addressed, and gaps in our knowledge bridged, if floristic diversity is to be conserved over the long term in New England forests.

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LITERATURE CITED

- BORMANN, F. H. AND G. E. LIKENS. 1979. *Pattern and Process in a Forested Ecosystem*. Springer-Verlag, New York.
- , T. G. SICCAMA, G. E. LIKENS, AND R. H. WHITTAKER. 1970. The Hubbard Brook ecosystem study: Composition and dynamics of the tree stratum. *Ecol. Monogr.* 40: 373–388.
- BRATTON, S. P. 1976. Resource division in an understory herb community: Responses to temporal and microtopographic gradients. *Amer. Naturalist* 110: 679–693.
- CARBONNEAU, L. E. 1986. Old-growth forest stands in New Hampshire: A

- preliminary investigation. M.S. thesis, Univ. New Hampshire, Durham, NH.
- CROZIER, C. R. AND R. E. J. BOERNER. 1984. Correlation of understory herb distribution patterns with microhabitats under different tree species in a mixed mesophytic forest. *Oecologia* 62: 337–343.
- FEDERER, C. A., L. D. FLYNN, C. W. MARTIN, J. W. HORNBECK, AND R. S. PIERCE. 1990. Thirty years of hydrometeorologic data at the Hubbard Brook Experimental Forest, New Hampshire. Gen. Tech. Rep. NE-141, U.S.D.A. Forest Service, Northeastern Forest Exp. Sta., Radnor, PA.
- HUBBARD BROOK EXPERIMENTAL FOREST. 1996. Hubbard Brook Ecosystem study site description and research activities, 2nd ed. Rep. NE-INF-96-96R, U.S.D.A. Forest Service, Northeastern Forest Exp. Sta., Radnor, PA.
- KARTESZ, J. T. 1994. A Synonymized Checklist of the Vascular Flora of the United States, Canada, and Greenland, 2nd ed., Vol. 2. Timber Press, Portland, OR.
- KIMMINS, J. P. 1997. *Forest Ecology: A Foundation for Sustainable Management*, 2nd ed. Prentice-Hall, Upper Saddle River, NJ.
- LEAK, W. B. 1987. Characteristics of five climax stands in New Hampshire. Res. Note NE-336, U.S.D.A. Forest Service, Northeastern Forest Exp. Sta., Radnor, PA.
- LIKENS, G. E. AND F. H. BORMANN. 1995. *Biogeochemistry of a Forested Ecosystem*, 2nd ed. Springer-Verlag, New York.
- MACARTHUR, R. H. AND E. O. WILSON. 1963. An equilibrium theory of insular zoogeography. *Evolution* 17: 373–387.
- MARTIN, C. W. AND J. W. HORNBECK. 1989. Revegetation after strip cutting and block clearcutting in northern hardwoods: A 10-year history. Res. Pap. NE-625, U.S.D.A. Forest Service, Northeastern Forest Exp. Sta., Radnor, PA.
- MEIER, A. J., S. P. BRATTON, AND D. C. DUFFY. 1995. Biodiversity in the herbaceous layer and salamanders in Appalachian primary forests, pp. 236–246. *In*: J. Davis, ed., *Eastern Old-Growth: Prospects for Rediscovery and Recovery*. Island Press, Washington, DC.
- MUELLER-DUMBOIS, D. AND H. ELLENBERG. 1974. *Aims and Methods of Vegetation Ecology*. John Wiley & Sons, Inc., New York.
- OSTLE, B. AND R. W. MENSIG. 1975. *Statistics in Research*, 3rd ed. Iowa State Univ. Press, Ames, IA.
- PALMER, M. W., G. L. WADE, AND P. NEAL. 1995. Standard for the writing of floras. *BioScience* 45: 339–345.
- PETERKEN, G. F. AND M. GAME. 1984. Historical factors affecting the number and distribution of vascular plant species in central Lincolnshire. *J. Ecol.* 72: 155–182.
- SICCAMA, T. G., F. H. BORMANN, AND G. E. LIKENS. 1970. The Hubbard Brook Ecosystem Study: Productivity, nutrients, and phytosociology of the herbaceous layer. *Ecol. Monogr.* 40: 389–402.
- TEELING, L. M. 1998. The Floristic Diversity of the Experimental Watersheds of the Hubbard Brook Experimental Forest, New Hampshire. M.S. thesis, Univ. New Hampshire, Durham, NH.
- WESTVELD, M., R. I. ASHMAN, H. I. BALDWIN, R. P. HOLDSWORTH, R. S. JOHN-

- SON, J. H. LAMBERT, H. J. LUTZ, L. SWAIN, AND M. STANDISH. 1956. Natural forest vegetation zones of New England. *J. Forest.* (Washington) 34: 332–338.
- WHITNEY, G. G. 1991. Relation of plant species to substrate, landscape position, and aspect in north central Massachusetts. *Canad. J. Forest Res.* 21: 1245–1252.
- AND D. R. FOSTER. 1988. Overstorey composition and the determinants of the understorey flora of woods of central New England. *J. Ecol.* 76: 867–876.
- WHITTAKER, R. H., F. H. BORMANN, G. E. LIKENS, AND T. G. SICCAMA. 1974. The Hubbard Brook Ecosystem Study: Forest biomass and production. *Ecol. Monogr.* 44: 233–252.

APPENDIX

CHECKLIST OF THE VASCULAR FLORAS OF THE SEVEN HUBBARD BROOK EXPERIMENTAL WATERSHEDS

Nomenclature conforms to Kartesz (1994). Non-native species are indicated by an asterisk (*). Woodland herbaceous species are indicated by a cross (+). Watersheds on the south to southeastern-facing slope are represented by W1, W3, W4, W5, and W6, while W7 and W8 represent watersheds on the north-facing slope.

| | W1 | W3 | W4 | W5 | W6 | W7 | W8 |
|---|----|----|----|----|----|----|----|
| PTERIDOPHYTA | | | | | | | |
| DENNSTAEDTIACEAE | | | | | | | |
| + <i>Dennstaedtia punctilobula</i> (Michx.) Moore | × | × | × | × | × | × | × |
| DRYOPTERIDACEAE | | | | | | | |
| + <i>Athyrium filix-femina</i> (L.) Roth | | | | | × | × | × |
| + <i>Dryopteris</i> × <i>boottii</i> (Tuck.) Underw. | | | | | | × | × |
| + <i>Dryopteris campyloptera</i> Clarkson | | | | × | | × | × |
| + <i>Dryopteris carthusiana</i> (Vill.) H. P. Fuchs | × | × | × | × | × | × | × |
| <i>Dryopteris intermedia</i> (Muhl. ex Willd.) A. Gray | × | × | × | × | × | × | × |
| + <i>Gymnocarpium dryopteris</i> (L.) Newman | | | | | | × | × |
| + <i>Onoclea sensibilis</i> L. | | × | × | × | | × | |
| + <i>Polystichum acrostichoides</i> (Michx.) Schott | | | × | | | | × |
| EQUISETACEAE | | | | | | | |
| + <i>Equisetum arvense</i> L. | | | × | | | × | |
| + <i>Equisetum sylvaticum</i> L. | | | | × | | | |

APPENDIX

Continued.

| | W1 | W3 | W4 | W5 | W6 | W7 | W8 |
|---|----|----|----|----|----|----|----|
| LYCOPODIACEAE | | | | | | | |
| + <i>Huperzia lucidula</i> (Michx.) Trevis. | × | × | × | × | × | × | × |
| + <i>Lycopodium annotinum</i> L. | | × | | | | | |
| + <i>Lycopodium clavatum</i> L. | | | × | × | | × | × |
| + <i>Lycopodium obscurum</i> L. | × | × | × | × | | × | × |
| OPHIOGLOSSACEAE | | | | | | | |
| + <i>Botrychium oneidense</i> (Gilbert) House | | | | | × | | |
| OSMUNDACEAE | | | | | | | |
| + <i>Osmunda cinnamomea</i> L. | | | | × | | × | × |
| + <i>Osmunda claytoniana</i> L. | × | × | × | × | × | × | × |
| POLYPODIACEAE | | | | | | | |
| + <i>Polypodium virginianum</i> L. | × | × | | | | × | |
| THELYPTERIDACEAE | | | | | | | |
| + <i>Phegopteris connectilis</i> (Michx.) Watt | × | × | × | × | × | × | × |
| + <i>Thelypteris noveboracensis</i> (L.) Nieuwl. | × | × | × | × | × | × | × |
| PINOPHYTA (Gymnosperms) | | | | | | | |
| PINACEAE | | | | | | | |
| <i>Abies balsamea</i> (L.) P. Mill. | × | × | × | × | × | × | × |
| <i>Picea rubens</i> Sarg. | × | × | × | × | × | × | × |
| <i>Pinus strobus</i> L. | | | | × | | | |
| <i>Tsuga canadensis</i> (L.) Carrière | | × | × | × | × | × | × |
| TAXACEAE | | | | | | | |
| <i>Taxus canadensis</i> Marshall | | | × | | × | | |
| MAGNOLIOPHYTA (Angiosperms) | | | | | | | |
| MAGNOLIOPSIDA (Dicots) | | | | | | | |
| ACERACEAE | | | | | | | |
| <i>Acer pensylvanicum</i> L. | × | × | × | × | × | × | × |
| <i>Acer rubrum</i> L. | × | × | × | × | × | × | × |
| <i>Acer saccharum</i> Marshall | × | × | × | × | × | × | × |
| <i>Acer spicatum</i> Lam. | × | × | × | × | × | × | × |
| ARALIACEAE | | | | | | | |
| + <i>Aralia hispida</i> Vent. | | | | × | | | |
| + <i>Aralia nudicaulis</i> L. | × | × | × | × | × | × | × |
| + <i>Aralia racemosa</i> L. subsp. <i>racemosa</i> | × | | × | × | | | |
| + <i>Panax trifolius</i> L. | | | | | × | | |
| ASTERACEAE | | | | | | | |
| <i>Anaphalis margaritacea</i> (L.) Benth. & Hook. f. | | | | × | | | |

APPENDIX

Continued.

| | W1 | W3 | W4 | W5 | W6 | W7 | W8 |
|--|----|----|----|----|----|----|----|
| + <i>Aster acuminatus</i> Michx. | × | × | × | × | × | × | × |
| <i>Aster lateriflorus</i> (L.) Britton | | | × | × | | | |
| + <i>Aster macrophyllus</i> L. | × | | | | | | |
| <i>Euthamia graminifolia</i> (L.) Nutt. | | | × | × | | × | |
| * <i>Hieracium aurantiacum</i> L. | | | | × | | × | |
| * <i>Hieracium caespitosum</i> Dumort. | | | × | × | | | |
| <i>Hieracium scabrum</i> Michx. | | | | × | | | |
| <i>Lactuca hirsuta</i> Muhl. ex Nutt. var. <i>sanguinea</i> (Bigelow) Fernald | | | × | | | | |
| + <i>Prenanthes altissima</i> L. | × | × | × | × | × | × | × |
| + <i>Senecio aureus</i> L. | | | | × | | | |
| <i>Solidago canadensis</i> L. var. <i>canadensis</i> | | | × | × | | | |
| + <i>Solidago macrophylla</i> Pursh | × | × | × | × | × | × | × |
| <i>Solidago rugosa</i> P. Mill. subsp. <i>rugosa</i> var. <i>rugosa</i> | × | × | × | × | | × | |
| * <i>Taraxacum officinale</i> (L.) G. H. Weber ex F. H. Wigg. | | | | × | | | |
| BALSAMINACEAE | | | | | | | |
| + <i>Impatiens capensis</i> Meerb. | | | | | | × | |
| BETULACEAE | | | | | | | |
| <i>Betula alleghaniensis</i> Britton | × | × | × | × | × | × | × |
| <i>Betula cordifolia</i> Regel | × | × | × | × | × | × | × |
| <i>Betula papyrifera</i> Marshall | × | × | × | × | | × | × |
| <i>Betula populifolia</i> Marshall | | × | × | × | | × | × |
| <i>Ostrya virginiana</i> (P. Mill.) K. Koch | | | | | | × | |
| CAMPANULACEAE | | | | | | | |
| <i>Lobelia inflata</i> L. | | | | × | | | |
| CAPRIFOLIACEAE | | | | | | | |
| <i>Diervilla lonicera</i> P. Mill. | | | × | × | | | |
| <i>Lonicera canadensis</i> Bartram ex Marshall | × | × | × | × | × | × | × |
| <i>Sambucus racemosa</i> L. subsp. <i>pubens</i> (Michx.) House var. <i>pubens</i> (Michx.) Koehne | × | × | × | × | × | × | × |
| <i>Viburnum alnifolium</i> Marshall | × | × | × | × | × | × | × |
| CLUSIACEAE | | | | | | | |
| * <i>Hypericum perforatum</i> L. | | | | × | | | |
| CORNACEAE | | | | | | | |
| <i>Cornus alternifolia</i> L. f. | × | × | × | × | × | × | |
| + <i>Cornus canadensis</i> L. | × | × | × | × | × | × | × |

APPENDIX

Continued.

| | W1 | W3 | W4 | W5 | W6 | W7 | W8 |
|--|----|----|----|----|----|----|----|
| DROSERACEAE | | | | | | | |
| <i>Drosera rotundifolia</i> L. | | | | × | | | |
| ERICACEAE | | | | | | | |
| + <i>Gaultheria hispidula</i> (L.) Muhl. ex Bigelow | | | | | | | × |
| <i>Vaccinium angustifolium</i> Aiton | | | | | | × | |
| <i>Vaccinium myrtilloides</i> Michx. | | | | | × | × | × |
| FAGACEAE | | | | | | | |
| <i>Fagus grandifolia</i> Ehrh. | × | × | × | × | × | × | × |
| FUMARIACEAE | | | | | | | |
| + <i>Dicentra canadensis</i> (Goldie) Walp. | | × | | | | | |
| GROSSULARIACEAE | | | | | | | |
| <i>Ribes cynosbati</i> L. | × | × | | × | | | |
| <i>Ribes glandulosum</i> Grauer | × | × | × | × | × | × | × |
| LAMIACEAE | | | | | | | |
| + <i>Scutellaria lateriflora</i> L. | | | | | | × | |
| MONOTROPACEAE | | | | | | | |
| + <i>Monotropa uniflora</i> L. | × | × | × | × | × | × | × |
| OLEACEAE | | | | | | | |
| <i>Fraxinus americana</i> L. | × | × | × | × | × | × | × |
| ONAGRACEAE | | | | | | | |
| + <i>Circaea alpina</i> L. | | | | | | × | |
| <i>Epilobium coloratum</i> Biehler | | | | × | | | |
| OROBANCHACEAE | | | | | | | |
| + <i>Epifagus virginiana</i> (L.) W. Bar- tram | × | × | × | | × | | |
| OXALIDACEAE | | | | | | | |
| + <i>Oxalis montana</i> Raf. | × | × | × | × | × | × | × |
| <i>Oxalis stricta</i> L. | | | | × | | | |
| POLYGONACEAE | | | | | | | |
| <i>Polygonum cilinode</i> Michx. | × | × | | | | | |
| PORTULACACEAE | | | | | | | |
| + <i>Claytonia caroliniana</i> Michx. var. <i>caroliniana</i> | | | | × | | × | |
| PRIMULACEAE | | | | | | | |
| + <i>Trientalis borealis</i> Raf. | × | × | × | × | × | × | × |

APPENDIX

Continued.

| | W1 | W3 | W4 | W5 | W6 | W7 | W8 |
|--|----|----|----|----|----|----|----|
| RANUNCULACEAE | | | | | | | |
| + <i>Actaea pachypoda</i> Elliott | | × | × | | | | |
| + <i>Anemone quinquefolia</i> L. | | × | | | | | |
| + <i>Coptis trifolia</i> (L.) Salisb. subsp. <i>groenlandica</i> (Oeder) Hultén | × | | × | × | | × | × |
| + <i>Thalictrum pubescens</i> Pursh | | | | × | | | × |
| ROSACEAE | | | | | | | |
| <i>Amelanchier bartramiana</i> (Tausch) M. Roem. | | | | × | | × | |
| <i>Fragaria virginiana</i> Duchesne | | | | × | | | |
| <i>Potentilla simplex</i> Michx. | | | | × | | | |
| <i>Prunus pensylvanica</i> L. f. | × | × | × | × | | × | × |
| <i>Rubus elegantulus</i> Blanch. | × | × | × | × | | × | × |
| + <i>Rubus hispidus</i> L. | | | | × | | | |
| <i>Rubus idaeus</i> L. subsp. <i>strigosus</i> (Michx.) Focke | × | × | × | × | × | × | × |
| + <i>Rubus pubescens</i> Raf. | | | | | | × | × |
| <i>Sorbus americana</i> Marshall | × | × | × | × | × | × | × |
| <i>Spiraea alba</i> Du Roi var. <i>latifolia</i> (Aiton) Dippel | | | | × | | × | |
| <i>Spiraea tomentosa</i> L. | | | | × | × | | |
| RUBIACEAE | | | | | | | |
| + <i>Galium asprellum</i> Michx. | | × | × | × | × | × | |
| + <i>Galium triflorum</i> Michx. | | | × | | | | |
| + <i>Mitchella repens</i> L. | × | × | × | × | × | × | × |
| SALICACEAE | | | | | | | |
| <i>Populus grandidentata</i> Michx. | | | | × | | | |
| <i>Populus tremuloides</i> Michx. | | | × | × | | | |
| <i>Salix bebbiana</i> Sarg. | | × | × | × | | | |
| <i>Salix discolor</i> Muhl. | | | | × | | | |
| <i>Salix humilis</i> Marshall | | | | × | | | |
| SAXIFRAGACEAE | | | | | | | |
| + <i>Chrysosplenium americanum</i> Schwein. ex Hook. | | | | | × | | |
| + <i>Tiarella cordifolia</i> L. | | | | | | × | |
| SCROPHULARIACEAE | | | | | | | |
| + <i>Chelone glabra</i> L. | | | | × | | × | |
| VIOLACEAE | | | | | | | |
| + <i>Viola macloskeyi</i> F. E. Lloyd subsp. <i>pallens</i> (Banks ex DC.) M. S. Baker | × | × | × | × | × | × | × |
| + <i>Viola rotundifolia</i> Michx. | × | × | | × | × | × | × |

APPENDIX

Continued.

| | W1 | W3 | W4 | W5 | W6 | W7 | W8 |
|--|----|----|----|----|----|----|----|
| LILIOPSIDA (Monocots) | | | | | | | |
| ARACEAE | | | | | | | |
| + <i>Arisaema triphyllum</i> (L.) Schott subsp. <i>triphyllum</i> | × | × | × | × | | | |
| CYPERACEAE | | | | | | | |
| + <i>Carex arctata</i> W. Boott ex Hook. | × | × | × | × | × | × | × |
| + <i>Carex brunnesens</i> (Pers.) Poir. | × | × | × | × | | × | × |
| + <i>Carex communis</i> Bailey | × | | × | × | | | |
| + <i>Carex deflexa</i> Hornem. | × | × | × | | | | |
| + <i>Carex gynandra</i> Schwein. | | × | × | × | × | × | × |
| + <i>Carex intumescens</i> Rudge | × | × | × | × | × | × | × |
| + <i>Carex leptonevia</i> (Fernald) Fernald | × | | × | | × | × | × |
| + <i>Carex lurida</i> Wahlenb. | | | | × | | | |
| + <i>Carex scabrata</i> Schwein. | | | | × | | × | |
| <i>Carex scoparia</i> Schkuhr ex Willd. | × | | × | × | | × | |
| <i>Scirpus atrocinctus</i> Fernald | | | | × | | | |
| <i>Scirpus atrovirens</i> Willd. | | | | × | | | |
| <i>Scirpus cyperinus</i> (L.) Kunth | | × | × | × | | × | |
| JUNCACEAE | | | | | | | |
| <i>Juncus brevicaudatus</i> (Engelm.) Fernald | | | | × | | × | |
| <i>Juncus effusus</i> L. | | | | | | | |
| <i>Juncus tenuis</i> Willd. | | | | × | | | |
| LILIACEAE | | | | | | | |
| + <i>Clintonia borealis</i> (Aiton) Raf. | × | × | × | × | × | × | × |
| + <i>Erythronium americanum</i> Ker Gawl. | × | × | × | × | × | × | × |
| + <i>Maianthemum canadense</i> Desf. | × | × | × | × | × | × | × |
| + <i>Medeola virginiana</i> L. | × | × | × | × | × | × | × |
| + <i>Polygonatum pubescens</i> (Willd.) Pursh | × | × | × | × | | | |
| + <i>Smilacina racemosa</i> (L.) Desf. | × | × | × | × | × | × | × |
| + <i>Streptopus amplexifolius</i> (L.) DC. | | | | | | × | × |
| + <i>Streptopus roseus</i> Michx. | × | × | × | × | × | × | × |
| + <i>Trillium erectum</i> L. | × | × | × | × | × | × | × |
| + <i>Trillium undulatum</i> Willd. | × | × | × | × | × | × | × |
| + <i>Uvularia sessilifolia</i> L. | × | × | × | × | × | × | × |
| + <i>Veratrum viride</i> Aiton | | | | | | × | |
| ORCHIDACEAE | | | | | | | |
| + <i>Corallorhiza maculata</i> (Raf.) Raf. | | | × | | | | × |
| + <i>Cypripedium acaule</i> Aiton | | × | | | | × | × |

APPENDIX

Continued.

| | W1 | W3 | W4 | W5 | W6 | W7 | W8 |
|---|----|----|----|----|----|----|----|
| + <i>Goodyera repens</i> (L.) R. Br. ex Aiton f. | | | | | | | |
| + <i>Platanthera orbiculata</i> (Pursh) Lindl. | | | | | × | | |
| POACEAE | | | | | | | |
| <i>Agrostis scabra</i> Willd. | × | | × | × | | | |
| <i>Agrostis gigantea</i> Roth | | | × | × | | | |
| + <i>Brachyelytrum septentrionale</i> (Babel) G. C. Tucker | × | × | | × | | × | |
| <i>Calamagrostis canadensis</i> (Michx.) P. Beauv. var. <i>canadensis</i> | | | | × | | | |
| + <i>Cinna latifolia</i> (Trevir ex R. Goebb.) Griseb. | × | × | × | × | × | × | |
| <i>Danthonia compressa</i> Austin ex Peck | | | × | × | | | × |
| <i>Danthonia spicata</i> (L.) F. Beauv. ex Roem. & Schult. | | × | × | | | | |
| <i>Deschampsia cespitosa</i> (L.) P. Beauv. | | | | | | × | |
| * <i>Festuca ovina</i> L. | | | × | | | | |
| <i>Glyceria melicaria</i> (Michx.) F. T. Hubb. | | | | | | × | |
| <i>Glyceria striata</i> (Lam.) Hitchc. | | | | × | | | |
| <i>Panicum lanuginosum</i> Elliott var. <i>fasciculatum</i> (Torr.) Fernald | | × | | × | × | | |